Enemy release and evolution of increased competitive ability: At last, a smoking gun!

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Evolution by natural selection can sometimes be very rapid and therefore relevant for many ecological questions (Schoener, 2011). One area of ecology where this appears to be particularly true are biological invasions, probably because species introductions often involve major changes in biotic interactions and thus novel environments with different selective forces than in the species' native ranges. The study of evolutionary changes in invasive species has recently become an extremely active area of research (Bossdorf *et al.*, 2005; Prentis *et al.*, 2008), and one of the key hypotheses that stimulated this research is the evolution of increased competitive ability (EICA) hypothesis (Blossey & Nötzold, 1995). It proposes that release from natural enemies, and subsequent evolution of more competitive genotypes, may explain the increased performance of dominant plant invaders in their introduced ranges. Although the original EICA paper has now been cited over 500 times, and numerous studies examined the (putative) consequences of EICA by comparing growth, competitive ability and/or herbivore defence of native and introduced populations in common environments, with mixed results (see e.g., Bossdorf *et al.*, 2005; Colautti *et al.*, 2009), there has been surprisingly little proof of EICA "in action". On page xxx of this issue of the *New Phytologist*, Uesugi & Kessler (2013) now present experimental evidence that release from above-ground herbivory can indeed cause rapid evolution of increased plant competitive ability, and they therefore provide an important "smoking gun" for the proposed evolutionary mechanism underlying the EICA hypothesis.

Uesugi & Kessler (2013) studied tall goldenrod (*Solidago altissima*), a perennial plant native to North America but highly invasive in Europe and other parts of the world. They studied goldenrod in its native range, in a 12-year herbivore-exclosure experiment in an old field in the North-eastern US (Fig. 1). Since all study plots were initially established from the same goldenrod genotypes, any genetic differentiation observed between herbivore-exclusion and control plots can be causally linked to the experimental treatments, and it is thus evidence

of rapid evolution in response to changes in herbivory. Uesugi and Kessler sampled offspring from each of the study plots and showed that in a common environment, goldenrod plants from herbivore-exclusion plots performed significantly better in the presence of interspecific competitors, and had substantially higher root concentrations of polyacetylenes, putative allelopathic agents of goldenrod, than plants from control plots. They also show that the most abundant of the polyacetylenes strongly reduces germination and growth of the interspecific competitor in the bioassay. Taken together, this demonstrates that the release from natural enemies created by insecticides caused rapid evolution of increased competitive ability in goldenrod, and it strongly suggests that the underlying mechanism might be selection for increased production of polyacetylene, an allelochemical suppressing interspecific competitors.

One intriguing aspect of the study of Uesugi and Kessler is that it elegantly links and in fact unifies two of the most popular hypotheses attempting to explaining plant invasiveness, the EICA hypothesis and the Novel Weapons Hypothesis (Callaway & Ridenour 2004), which proposes that some highly invasive plants may be dominant because they possess novel allelochemicals to which their new neighbours have not been exposed to in the past, and which therefore have particularly strong negative effects on these natives.

Callaway & Ridenour (2004) already pointed out the possible link between novel weapons and EICA. They hypothesized that if allelopathy indeed confers a substantial fitness advantage, it might evolve rapidly after enemy release and could therefore in some cases be the key mechanism underlying EICA. However, at this time no empirical evidence existed for such an evolutionary change, and the EICA and Novel Weapons Hypothesis have largely been studied independently since then. Still, a link between enemy release, EICA and novel weapons is very likely, because both enemy release and novel weapons are expected to be strongly influenced by the phylogenetic distinctness of plant invaders (Fig. 2).

Introduced plants that are phylogenetically distinct from their recipient communities are not only more likely to possess novel allelochemicals but also a chemical defence novel to the herbivores in the introduced range. As a consequence, phylogenetically distinct invaders experience greater enemy release (e.g., Cappuccino & Carpenter 2005; Hill & Kotanen 2009; Ness *et al.*, 2011), and they should thus not only possess novel weapons but also the means for their rapid evolutionary increase. Because of this double advantage we should expect evolution of increased allelopathy to be common in phylogenetically distinct invaders, and it may well contribute to the frequently observed associations between phylogenetic novelty, chemical novelty and plant invasion success (e.g., Cappuccino & Arnason, 2006; Strauss *et al.*, 2006).

Of course the study of Uesugi & Kessler (2013) has not been done in invasive populations, but in a native population of goldenrod, and it is now important to test whether evolution of increased allelopathy indeed also occurred in response to natural enemy release. Of course the interpretation of Uesugi & Kessler's results rests on the assumption of a trade-off between allocation to defence versus allelopathy, and their study did not provide any formal proof that such a trade-off exists. Providing these missing pieces of evidence will be crucial next steps towards understanding goldenrod invasion. Another important direction for future research should be to test for increased allelopathy of invasive populations across multiple invasive species, connect these data to phylogenetic distance, enemy release and invasion success, and thereby test the generality of Uesugi and Kessler's findings.

Even though evolution experiments are the gold standard for testing eco-evolutionary hypotheses, and their usefulness for ecologists has long been recognised (e.g., Conner, 2003), evolution experiments in the field are still quite rare (Kawecki *et al.*, 2012). The study of Uesugi & Kessler (2013), together with other recent studies (e.g., Agrawal *et al.*, 2012), clearly demonstrates the power of the experimental evolution approach. It also shows the

strength of combining multiple approaches, in their case a long-term selection experiment in the field with common garden studies, bioassays and chemical analyses. Ultimately, it is such combinations of well-designed ecological and evolutionary experiments with thorough analyses of the underlying functional mechanisms – combining realism with precision, "why?" and "how?" questions – that most advance our understanding of ecological systems.

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Fig. 1. *Solidago altissim*a is common in old fields where it experiences strong intra- and interspecific competition.

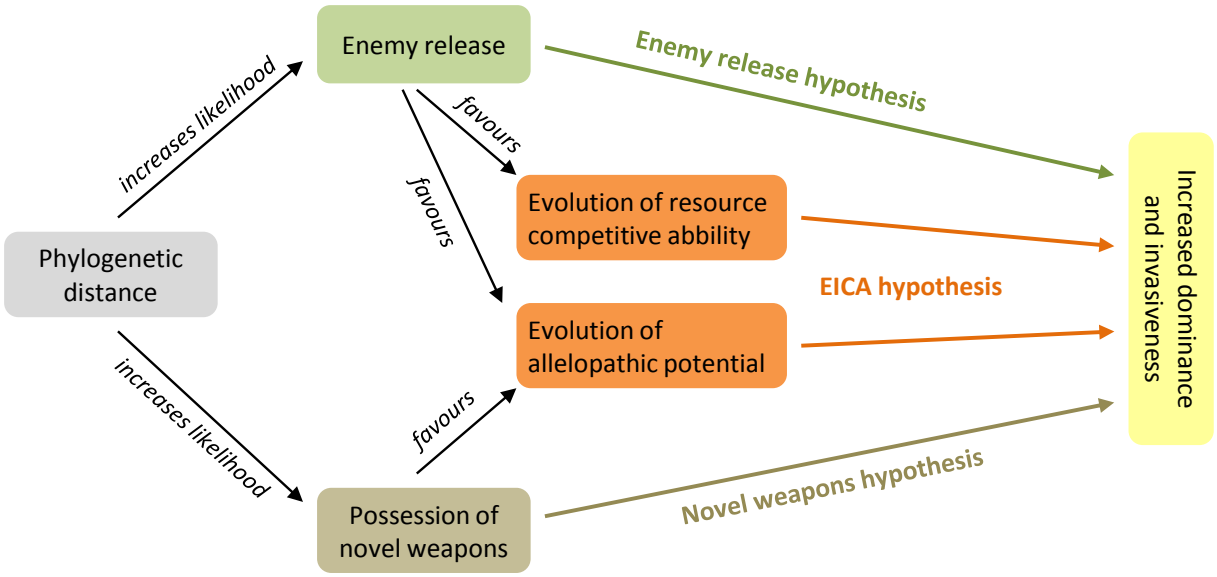

Fig. 2. Relationships between different hypotheses attempting to explain the increased dominance and invasiveness of plants in their introduced range.